REGIONAL GROWTH PATTERNS OF JUVENILE ALBACORE (*THUNNUS ALALUNGA*) IN THE EASTERN NORTH PACIFIC

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ABSTRACT

Population structure of North Pacific albacore (*Thunnus alalunga*) may be more complex than the current single-stock hypothesis given the apparent regional differences in size–at-age and movement patterns in the eastern North Pacific. In this study, otolith-based techniques were used to analyze the age structure, daily growth rates and hatch dates of 126 albacore collected from two regions in the eastern North Pacific (northern: >40°N and southern: <40°N) in July through October of 2010 and 2011. Juvenile albacore collected from the southern region had significantly larger size–at-age than those collected from the northern region over a similar age range examined (423–1254 days). No significant regional difference in growth rates of juvenile albacore was detected over the ages examined, suggesting processes occurring in the first year and a half of life may have been driving regional size–at-age differences. Back-calculated hatch dates suggest protracted spawning for fish from both regions ranging from February to September with peak hatch dates between April and July (73% of all fish). Results from this two-year study suggest that juvenile albacore length–at-age estimates in the eastern North Pacific are region-specific and may need to be considered for future life history studies and stock assessments.

INTRODUCTION

Albacore (*Thunnus alalunga*) are highly migratory predators with a cosmopolitan distribution (Sund et al. 1981). In the Pacific Ocean, albacore are separated into North and South Pacific stocks due to limited mixing across the equator and isolated spawning grounds (Nakamura 1969). In the North Pacific, albacore spawn in the central and western Pacific where many begin transoceanic migrations to utilize the highly productive California Current in the eastern North Pacific (Clemens and Craig 1965; Wetherall et al. 1981). The distribution and relative abundance of albacore in the eastern North Pacific varies latitudinally (Laurs and Lynn 1977; Laurs and Wetherall 1981; Wetherall et al. 1987; Childers et al. 2011) and it has been suggested that there are two subgroups of albacore: a north-

ern group based offshore of the Pacific Northwest of the United States and Canada and a southern group located offshore of southern California and Baja, Mexico (Laurs and Lynn 1977; Laurs and Wetherall 1981; Wetherall et al. 1987; Laurs and Lynn 1991). The dividing line between these two subgroups is considered to be associated with the Mendocino Escarpment located at 40°N. Albacore from the two subgroups have been reported to differ in size composition, growth rates, movement patterns, and peak spawning periods, which has led to the hypothesis that there may be two sub-stocks of albacore in the eastern North Pacific (Laurs and Wetherall 1981; Laurs and Lynn 1991; Barr 2009; Childers et al. 2011).

Stock structure is a key component of management, and current management of North Pacific albacore assumes a single stock in the North Pacific. Growth rates during the juvenile stage can be directly linked to survival and subsequent population dynamics of adult fish populations (Houde 1987). One of the best approaches to retrospectively examine early life history is using otolith-derived age and growth estimates based on the deposition of daily rings. To date, however, few studies have attempted to use daily otolith ageing to examine albacore in the eastern North Pacific (Wetherall et al. 1987) because the technique is technically challenging and labor intensive (Williams et al. 2013). Near-daily deposition of daily growth increments has been validated for North Pacific albacore (Laurs et al. 1985) and allows for relatively high precision in estimates of age, growth rates, and hatch dates.

In this study, otolith microstructure was used to examine regional growth rates and length–at-age estimates of juvenile albacore in the eastern North Pacific. The daily ages of fish were then used to back-calculate fish hatch date to estimate albacore spawning periods, which can be used to address the sub-stock hypothesis. Temporal differences in spawning may support the possibility of two sub-stocks because separate stocks are defined by separation in time and/or space. Ultimately, information on the life history and ecology of albacore in the eastern North Pacific will provide updated biological parameters useful for stock-assessment models.
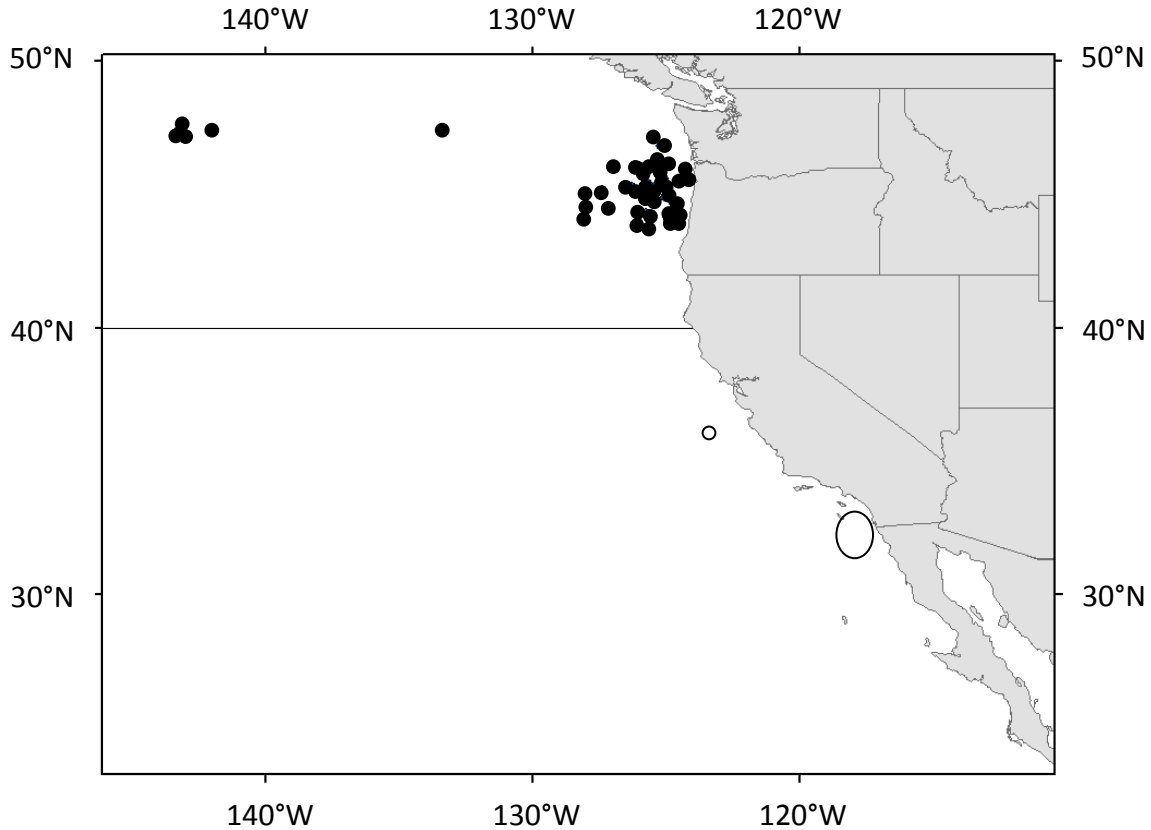
Figure 1.   Map of eastern North Pacific where the horizontal line at 40°N latitude represents the boundary between the northern and southern regions. Black solid circles represent location of samples collected from commercial fishing vessels in the northern region while the white ellipse represents location of samples collected from sport fishing vessels in the southern region. The single white circle in the southern region is the collection location of four individuals that were collected during a research-based tagging cruise.

MATERIALS AND METHODS

Study Area and Field Collections

The study area is located at the eastern extent of the North Pacific Gyre and is focused on two regions within the California Current during the summer and fall when albacore are targeted by local fisheries (Laurs and Lynn 1977) (fig. 1). The two regions are within the California Current and are exposed to coastal, wind–driven upwelling and are north and south of 40°N at the Mendocino Escarpment, defined as the northern and southern regions.

Albacore samples were collected from the north and south fishing regions from July through October of 2010 and 2011 (table 1). North samples were collected from commercial troll (artificial–jig fishing gears) and pole–and–line (live-bait fishing) surface fisheries targeting albacore. South samples were collected from recreational pole–and–line fishing vessels operating off southern California and Baja California, Mexico. All fish collected were frozen and transported to the NOAA Southwest Fisheries Science Center in La Jolla, California, for later processing.

Otolith Age and Growth

In the laboratory, albacore were measured to the nearest cm fork length (FL) and sagittal otoliths were removed from each fish, and cleaned following procedures described by Secor et al. 1991. One of the two otoliths was randomly chosen and embedded in low viscosity epoxy resin (fig. 2). After the epoxy resin hardened, the otolith was sectioned transversely using a Buehler isomet low-speed saw equipped with a diamond-wafering blade. Longitudinal sections were also performed on a subset of otoliths ($n = 20$); however, transverse sections produced the best product for counts. The otolith sections were mounted on glass slides with Crystalbond thermoplastic cement and polished with 0.3μm Alumina Alpha polish using 400 and 600 grit

TABLE 1
Summary of albacore samples collected and processed for otolith microstructure analysis during 2010 and 2011 from both the northern and southern regions.

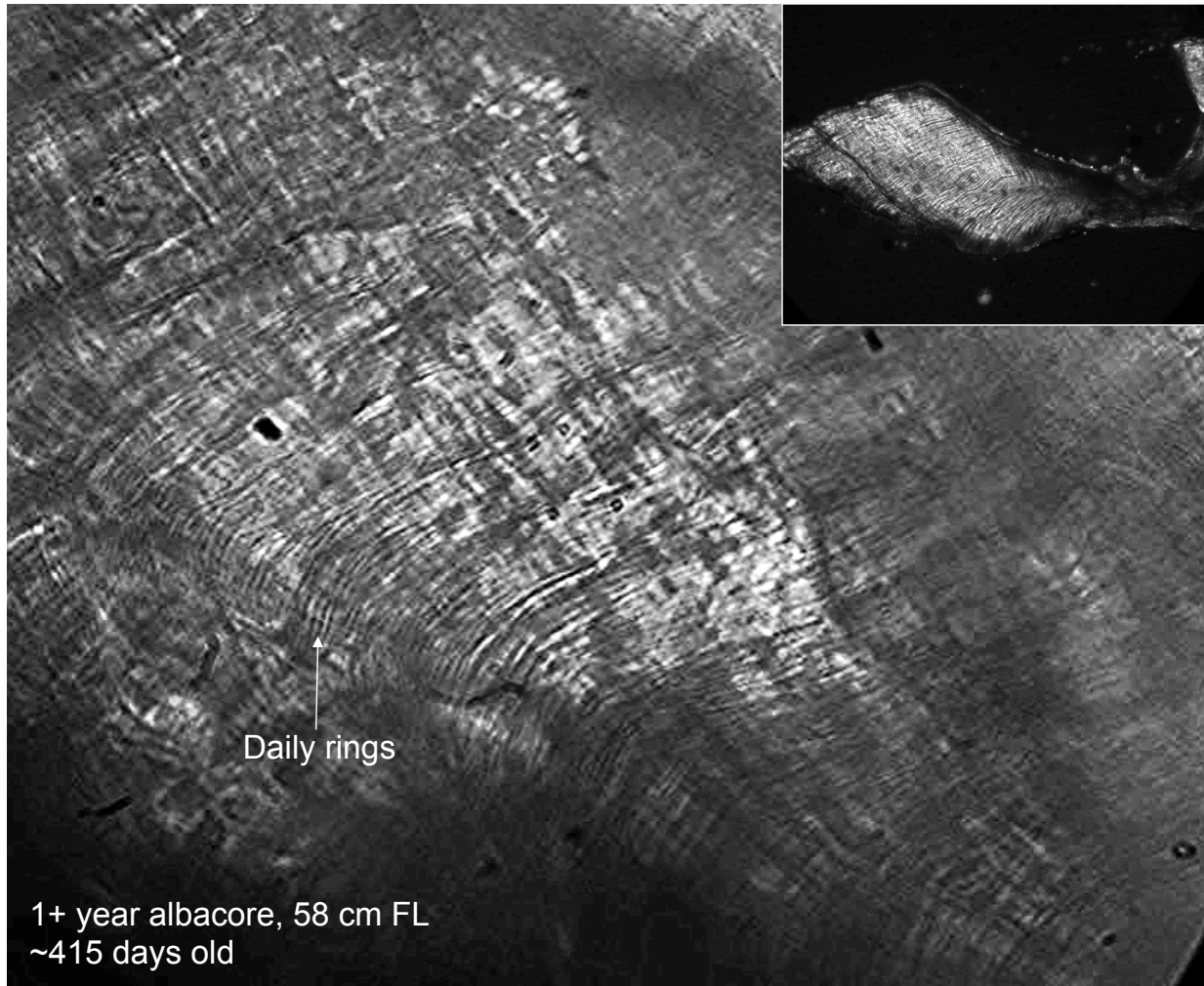| Region	2010	2011
North	42	46
South	34	4

Figure 2.   A transverse cross-section of the sagittal otolith from a year-1 albacore viewed at 65x with arrow illustrating a daily growth ring of the otolith microstructure. The image on the top right is a view of the entire otolith at 20x.

sandpaper until the core and daily increments were visible (Secor et al. 1991).

Otoliths were viewed with a Leica light microscope at 65× magnification and age was determined by counting daily growth increments from the outer margin to the core. The increments were counted with a Digital Imaging System (DIS). The DIS consisted of a Leica compound microscope, Diagnostic Instruments (2002) SPOT RT digital camera, a desktop computer with two 17-inch LCD monitors, and Image Pro-Plus (IP+) imaging software (Media Cybernetics 2002). The system was calibrated using a stage micrometer within the objective. The SPOT camera has an electronic shutter, which captures live image previews, allowing the user to fine focus and position the section of the otolith that is being imaged. The restricted field of view at this magnification required multiple images to be captured. After each photo, the stage was moved down towards the end of the previous image (i.e., the lead-ing edge of the previously captured image becomes the trailing edge of the next image). This process was repeated until arrays of images (15–20) were captured. All images were later resized and merged together in Adobe Photoshop CS5 to construct a final image. The "manual tag" tool was used in IP+ to count and label daily growth increments.

In some fish it was difficult to enumerate some of the inner increments near the core. To account for the inner increments that were unclear, a correction factor was applied to 5% of the fish from the northern region and 10% of the fish from the southern region. The correction factor was derived from several clear samples and was based on the relationship between fish age and otolith radius (Wells and Rooker 2004). To determine this relationship the radius was measured and the number of daily increments were counted on seven otoliths from the core to 40 days where inner increments were easily identified producing the following equation:
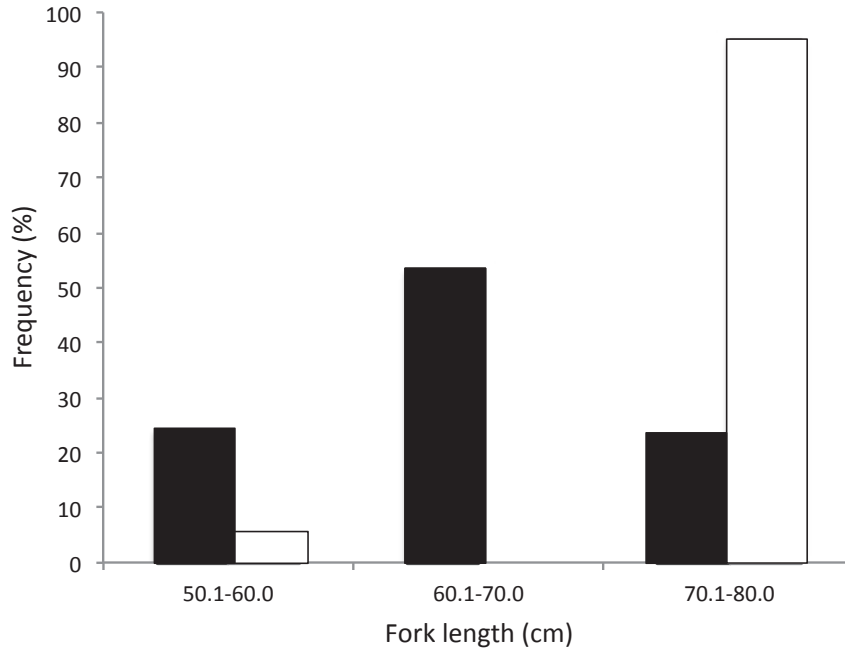
Figure 3.   Size distribution of albacore from the northern (black) and southern (white) regions.

Age$_p$ (days) = Age$_c$ (days) + [(otolith radius/ 564.14 μm) × (40 days)],

where Age$_p$ is the predicted (corrected) age, Age$_c$ is the increment count from the otolith reading, and 564.14 μm is the average otolith radius at 40 days of age. This correction factor was used to assist with age estimates for otoliths that were unclear and difficult to enumerate around the inner core area. This was accomplished by adding the predicted age from the unclear region (correction factor) to the increment count (number of identifiable increments).

A double-blind method was applied when ageing the otoliths. The otoliths were relabeled after sample preparation and a random number generator was used to select otoliths for ageing. Double-blind procedures prevented the reader from knowing any identifying characteristics of the sample (i.e., size, region, collection date). A single reader independently read each otolith three to four times until all age estimates were within 10%, and the average reading was taken as final. Differences in age estimates among three or more readings was evaluated by the average percent error (APE) (Beamish and Fournier 1981) and coefficient of variation (CV) (Chang 1982) to determine ageing precision in age estimates, CV is expressed as:

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j}$$

where X_{ij} is the ith age determination of the jth fish. X_j is the average age calculated for the jth fish and R is the number of times each individual is aged (Chang 1982).

Near-daily growth increments has been validated for North Pacific albacore using oxytetracycline mark and recapture, with an average growth rate of 0.954 increments per day (Laurs et al. 1985). To account for this discrepancy, a 4.6% increment adjustment change was applied to the raw data.

Data Analysis

The estimated age of each fish was subtracted from its date of capture to determine hatch dates and spawning periods for the northern and southern regions. Size-at–age relationships were analyzed using linear models to examine the relationship between fish age and fork length. Analysis of covariance (ANCOVA) was used to analyze regional differences in size-at-age (y-intercept) and growth rates (slopes) between albacore collected in the northern and southern regions. One model tested for size-at–age and growth differences for all albacore between each region, and an additional model was limited only to albacore of similar ages between the two regions (742–1254 days of age). Linearity was tested for the ANCOVA models; full ANCOVA models were first examined with region (factor), age (covariate), and the interaction term (region * age). Nonsignificant interaction terms ($p > 0.05$) were then removed from both models and only the reduced model was used for statistical interpretations. A single linear regression model
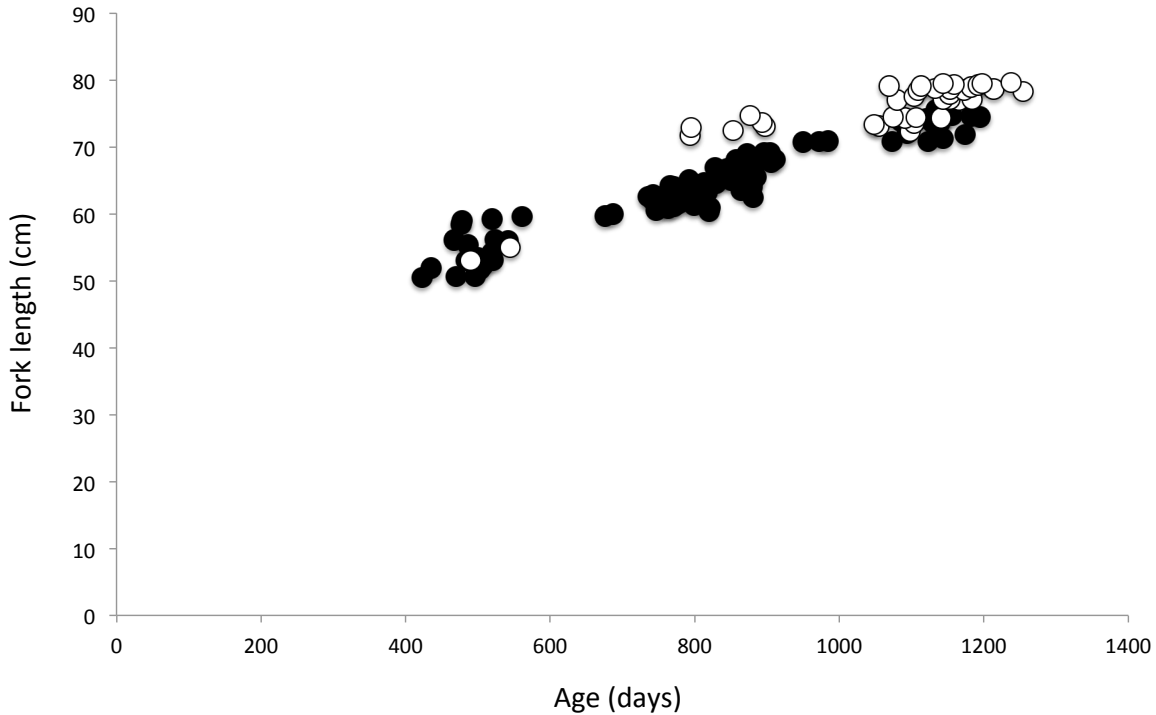
Figure 4.   Size-at-age relationship of albacore in the eastern North Pacific by region (northern region=black and southern region=white).

was also performed to provide an overall growth rate estimate for all albacore aged in this study. Analyses were conducted using the statistics software program SAS version 9.2 with $\alpha = 0.05$.

RESULTS

A total of 126 otoliths were collected from albacore in the eastern North Pacific from 2010 to 2011. From the north region, 87 otoliths were aged from fish 50.5 to 78.0 cm FL and from the southern region 36 otoliths were aged from fish ranging in size from 52.9 to 79.6 cm FL (tab. 1, fig. 3). Corresponding ages of all albacore ranged from 423 to 1254 days of age. The northern region was comprised of fish from 423 to 1095 days of age with 50% of the fish between 700 and 900 days of age. In the southern region, fish age ranged from 492 to 1254 days and was primarily dominated (70%) by fish of 1000 to 1200 days of age.

Precision of fish age estimates was assessed. For all age readings the CV for each region ranged from 0 to 6.88% and the APE was 1.07% and 0.34% for the northern and southern region, respectively. A CV value below 10% and an APE value below 5% comprise an acceptable ageing accuracy assessment between ageing estimates for many species and indicate a high level of precision between readings (Campana et al. 1995; Campana 2001).

Size-at-age estimates for albacore collected in the southern region were significantly larger than for fish in the northern region (ANCOVA; y-intercept; $p < 0.001$)

(fig. 4). These differences in fish size-at-age can be used as a proxy for regional growth rates, but the lack of a significant slope effect (ANCOVA; interaction term; $p > 0.05$) supports similar growth rates over the ages examined. Similarly, no significant regional growth rate difference (ANCOVA; interaction term; $p > 0.05$) was observed for albacore 742 to 1254 days of age. However, a significant size-at-age difference was found over this age range with larger fish in the south region (ANCOVA; y-intercept; $p < 0.001$) (fig. 4). A combined linear growth model of juvenile albacore resulted in an average growth rate of 0.03 cm per day over the size and age range examined (FL = 0.034[age] + 37.464; $r^2 = 0.893$).

Albacore hatch date distributions were protracted from February to September, with 73% of all fish hatched from April through July (fig. 5). Examination of albacore hatch dates between regions for fish hatched from 2007 through 2010 varied from year to year. In 2007, albacore in the northern region had peak hatching dates from May to August (87.5%) and in the southern region peak hatching dates ranged from April to July (81.4%). A similar range in hatch dates was observed in 2008. For the northern region, 20% of the fish hatched in May and 43.4% hatched in July through August, whereas 50% of the fish hatched from February through March and 37.5% hatched from May through June in the southern region. In 2009 and 2010, the majority of fish in the north region (69.2% and 77.7%) hatched from April to
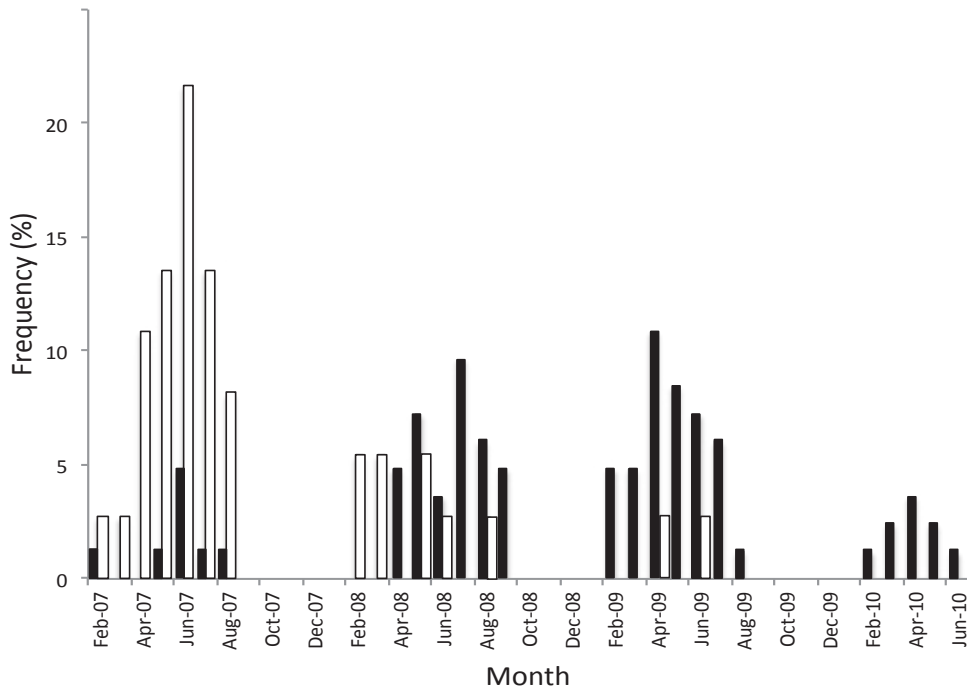
Figure 5. Albacore hatch date distributions in the eastern North Pacific by region (northern region=black and southern region=white).

July and March through May, respectively. Due to small sample sizes for fish in the southern region for 2009 and 2010, no hatching date estimates could be made.

DISCUSSION

Age estimates of juvenile albacore from the eastern North Pacific reveal a number of differences between fish in the northern and southern regions. Size and age distributions of albacore differed between fishing regions, with smaller and younger individuals (primarily age-2 and age-3) distributed in the northern region, while fish from the southern region were larger and older individuals (primarily age-3 and age-4). Thus, age is one factor accounting for regional size differences between the two regions. Hatch date distributions also reveal different year-class composition between regions sampled; primarily year class 2008 and 2009 for fish from the north and primarily 2007 for fish from the south. Another factor may be differences in growth rates at earlier life stages than examined here, as albacore had similar rates of growth at the ages analyzed in this study. Differences in albacore growth rates between regions have been found in previous studies with faster growth rates for fish in the southern region (Laurs and Wetherall 1981; Wetherall et al. 1987). In addition, South Pacific albacore demonstrate spatial variation in growth that may impact future stock assessment models (Williams et al. 2012).

Regional differences in oceanographic conditions that juvenile albacore are exposed to may affect growth and size. Juvenile albacore utilize the North Pacific Transition Zone (NPTZ) at the convergence between the subarctic and subtropical fronts to migrate eastward (Laurs and Lynn 1991). The dynamic Transition Zone Chlorophyll Front (TZCF) associated with the NPTZ acts as a migration route for many apex predators and seasonal shifts in these frontal zones have been shown to alter the movement and spatial distribution of tunas in the North Pacific into the highly productive California Current (skipjack, *Katsuwonus pelamis*; bigeye tuna, *Thunnus obesus*; bluefin tuna, *Thunnus orientalis*) (Boustany et al. 2010; Lehodey et al. 2008). At Cape Mendocino (~40°N), oceanic currents converge (Miller et al. 1999) creating conditions that result in alongshore transport influencing species diversity and productivity (Williams and Ralston 2002). Regions north and south of Cape Mendocino differ in sea surface temperature (SST), salinity and dissolved oxygen (NODC 2009). These differences are best observed using electronic tagging data that document the conditions at the location of the fish throughout the year. Tagging data obtained from both regions reveal important differences in both oceanography and migratory patterns for albacore from northern and southern regions (Childers et al. 2011). A focal area in the northern region was characterized by cool SST ($17.4 \pm 1.3°C$), high Chl-*a* concentrations (0.43 ± 0.44 mg m^{-3}), and a shallow mixed layer depth (mld) (≤ 25 m) in contrast to two focal areas in the southern region characterized by warmer SST ($18.9 \pm 1.4°C$, $20.7 \pm 0.6°C$), moderate to lower levels of Chl-*a* concentrations (0.32 ± 0.29 mg m^{-3}, 0.07 ± 0.02 mg m^{-3}), and a shallow to relatively deep mld (25.3 ± 0.9 m, 83.0 ± 37.0 m).

Numerous studies on tuna have indicated the importance of temperature for the early life stages of fish (Sund et al. 1981); however, this study can only infer the impact of environmental characteristics for juvenile albacore between the ages of one to three. A slight increase in SST has been shown to be advantageous to fish by resulting in faster growth rates, reduced mortality and early maturation (Higley et al. 1986; Neuheimer et al. 2011). Fish in the southern region, while residing in the California Current, inhabit an environment with warmer SST and an extended growing season facilitating faster growth rates than in the north (Hickling 1961; Bardarch et al. 1972). Similar results have been reported in several studies examining the relationship between SST, food availability, and tuna growth rates (Griffiths et al. 2009; Wexler et al. 2007; Wexler et al. 2011). Growth of juvenile southern bluefin tuna (*Thunnus maccoyi*) in the western Australian fishery is affected by SST, with larger sizes-at-age for fish exposed to the higher water temperatures associated with the Leeuwin Current (Leigh and Hearn 2000). However, albacore in the eastern North Pacific are not confined exclusively to the California Current, so conditions beyond this area will also influence growth rates.

Foraging ecology and associated energy intake can also influence growth rates and likely play a significant role in regional size-at-age trends observed for albacore. For marine mammals and fishes, foraging on prey species lower in caloric content has significant impacts on intraspecific growth rates and population dynamics which could impact fish growth rates (MacFarlane and Norton 2001; Glaser 2010). Several studies have quantified diets of albacore in the eastern North Pacific (McHugh 1952; Graham 1959; Iversen 1962; Pinkas et al. 1971; Bernard et al. 1985; Glaser 2010). Albacore are considered generalists with a diet largely composed of Pacific saury (*Cololabis saira*), northern anchovy (*Engraulis mordax*), cephalopods and euphausiids (McHugh 1952; Graham 1959; Iversen 1962; Pinkas et al. 1971; Bernard et al. 1985). Additionally, it has been shown that the albacore diet in the eastern North Pacific varies with respect to region; decapods, euphausiids, and anchovy dominate the diets in the north; and hake, saury, and anchovy are more dominant in the south (Glaser 2010). A diet dominated solely by fish species will typically have a higher caloric content than a mixed diet of fish and crustaceans. The energy content of decapods and euphausiids ranges from 2.5 to 3.2 kJg^{-1} in contrast to 3.5 to 7.9 kJg^{-1} for the fish species found in albacore stomachs (Glaser 2010). Consequently, albacore in the north may need to consume more prey in order to obtain the same amount of calories. Consuming greater quantities of prey species may result in increased energetic costs (i.e., migration and effort) and can have indirect influences on fish growth rates. Albacore in the northern region demonstrate extensive, horizontal movements to offshore areas with some individuals migrating into the central and western Pacific. In contrast, albacore in the southern region typically remain closer to the coast and often overwinter along the Baja peninsula, Mexico (Childers et al. 2011). The extensive migrations and reduced caloric content of the dominant prey items for fish in the northern region may have energetic costs that translate into less energy available for growth.

In addition to examining regional differences in growth, hatch dates can provide insight into temporal separation in spawning and stock structure. Albacore sampled in the eastern North Pacific were spawned during a protracted period from February through September with peak hatch dates (73%) occurring between April and July. This spawning period overlaps with previous estimates determined using otolith ageing and length-frequency analyses (Bigelow et al. 1993); however, Wetherall et al. 1987 reported evidence of winter spawning in the south region based on tag-recapture data of larger subadult (70–90 cm FL). A comparison of fish hatch dates between regions for the 2008 and 2009 cohorts did not yield any regional differences in this study. For both regions, sample sizes were limited and peak hatch dates were variable throughout spring and summer months suggesting that further collections over a longer time frame are needed to determine the potential for temporal separation in albacore spawning between regions.

This study demonstrates both the difficulty and the importance of understanding early life history characteristics of this commercially important fishery resource. Using otolith daily growth increment ageing, we have shown that juvenile albacore in the eastern North Pacific exhibit regional differences in length-at-age between the northern and southern regions, with larger fish in the south. Albacore size-at-age differences between regions may be a function of differing growth rates at earlier life stages since growth rates were similar over ages analyzed in this study. The spawning period of albacore in the eastern North Pacific was from February through September with 73% of all fish hatch dates occurring from April to July. Albacore growth is likely the result of multiple environmental (e.g., North Pacific Transition Zone, California Current System, El Niño-Southern Oscillation) and biological variables (e.g., migratory movements, diet) and may consequently vary based on region. These results support prior studies using alternative methods that suggest albacore in the two regions may represent different stocks; however, additional samples and information on spawning separation and how growth and recruitment are affected by temperature, productivity, and location of the TZCF are needed to

assess if two distinct stocks of albacore exist in the eastern North Pacific.

ACKNOWLEDGEMENTS

LITERATURE CITED

Alemany, F., L. Quintanilla, P. Velez-Belchí, A. García, D. Cortés, J. M. Rodríquez, M. L. Fernández de Puelles, C. González-Pola, and J. L. López-Jurado. 2010. Characterization of the spawning habitat of Atlantic bluefin tuna and related species n the Balearic Sea (western Mediterranean). Prog Oceanogr. 86: 21–38.

Ayers, J. M., and M. S. Lozier. 2010. Physical controls on the seasonal migration of the North Pacific transition zone chlorophyll front. J. Geophys. Res. 115: 1–11.

Ayón, P., M. I. Criales-Hernandez, R. Schwamborn, and H. J. Hirche. 2008. Zooplankton research off Peru: A review. Prog. Oceanogr. 79: 238–255.

Bakun, A., and K. Broad. 2003. Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. Fish. Oceanogr. 12: 458–473.

Balazik, M. T., G. C. Garman, M. L. Fine, C. H. Hager, and S. P. McIninch. 2010. Changes in age composition and growth characteristics of Atlantic sturgeon (Acipenser oxyrinchus oxyrinchus) over 400 years. Biol. Lett. 10: 1–4.

Barr, C. M. 2009. Are there two subgroups of albacore, Thunnus alalunga, in the North Pacific? Evidence from variability in catch, seasonal migrations, and length composition for two subgroups in the coastal fishery of North America. Master's thesis. Oregon State University: Oregon, USA.

Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 3: 982–983.

Bernard, H. J., J. B. Hedgepeth, and S. B. Reilly. 1985. Stomach contents of albacore, skipjack, and bonito caught off southern California during summer 1983. Cal Coop. Ocean. Fish. 26:175–182.

Bigelow, K. A., J. T. Jones, and M. M. Sierra. 1993. Age variability within a length-frequency mode of the North Pacific albacore fishery as determined by otolith analysis. Working paper prepared for North Pacific Albacore Workshop: 1–7.

Boustany, A. M., R. Matteson, M. Castleton, C. Farwell, and B. A. Block. 2010. Movements of Pacific bluefin tuna (Thunnus orientalis) in the Eastern North Pacific revealed with archival tags. Progr. Oceanogr. 86: 94–104.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish. Biol. 59: 197–242.

Campana, S. E., M. C. Annand, and J. I. McMillan. 2001. Graphical and statistical methods for determining the consistency of age determinations. T. Am. Fish. Soc. 124: 131–138.

Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39: 1208–1210.

Checkley, D. M., and J. A. Barth. 2009. Patterns and processes in the California Current system. Prog. Oceanogr. 83: 49–64.

Chen, K. S., P. R. Crone, and C. C. Hsu. 2010. Reproductive Biology of Thunnus alalunga. J. Fish. Biol. 77: 119–136.

Childers, J., S. Snyder, and S. Kohin. 2011. Migration and behavior of juvenile north Pacific albacore (Thunnus alalunga). Fish. Oceanogr. 20: 157–173.

Clemens, H. B. 1961. The migration, age, and growth of Pacific albacore (Thunnus germo), 1951–58. Fish B-NOAA. 115: 1–128.

Clemens, H. B., and W. L. Craig. 1965. An analysis of California's albacore fishery. Cali. Fish. Game. 128: 1–301.

Cury, P. 1994. Obstinate nature: An ecology of individuals. Thoughts on reproductive behavior and biodiversity. Can. J. Fish. Aquat. Sci. 51: 1664–1673.

Foreman, T. 1996. Estimates of age and growth, and an assessment of ageing techniques, for northern bluefin tuna, Thunnus thynnus, in the Pacific Ocean. IATTC. Bull. 21: 75–105.

Ganssle, D., and H. B. Clemens. 1953. California tagged albacore recovered off Japan. Cali. Fish. Game. 39: 443.

Gillanders, B. M., B. A. Black, M. G. Meekan, and M. A. Morrison. 2012. Climate effects on the growth of a temperate reef fish from the southern hemisphere: A biochronological approach. Mar. Biol. 195: 1327–1333.

Glaser, S. M. 2010. Interdecadal variability in predator-prey interactions of juvenile North Pacific albacore in the California Current System. Mar. Ecol. Prog. Ser. 414: 209–221.

Graham, J. J.1959. Northeastern Pacific albacore survey. Part 1. Biological observations. Report. No. Fisheries No: 310.

Griffiths, S. P., G. C. Fry, F. J. Manson, and D. C. Lou. 2009. Age and growth of longtail tuna (Thunnus tonggol) in tropical and temperate waters of the central Indo-Pacific. ICES. J. Mar. Sci. 67: 125–134.

Hickling, C. F. 1961. Tropical island fisheries longmans. Green and Co Ltd. London and Southampton, 287 pp.

Higley, L. G., L. P. Pedigo, and K. R. Ostlie. 1986. DEGDAY: A program for calculating degree days, and assumptions behind the degree-day approach. Envi. Entomol. 15: 999–1016.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. S. S. 2: 17–29.

Houde, E. D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87: 471–495.

Houde, E. D. 1993. Differences between marine and freshwater fish larvae: Implications for recruitment. ICES. J. Mar. Sci. 51: 91–97.

Houde, E. D., and C. E. Zastrow. 1993. Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. Bull. Mar. Sci. 53: 290–335.

Ichinokawa, M., A. L. Coan and Y. Takeuchi. 2008. Transoceanic migration rates of young North Pacific albacore, Thunnus alalunga from conventional tagging data. Can. J. Fish. Aquat Sci. 65: 1681–1691.

Iversen, R. T. B. 1962. Food of albacore tuna, Thunnus germo (Lacepede), in the central and northeastern Pacific. Fish. Bull. 62: 459–481.

Joseph, J. 2003. Managing fishing capacity of the world tuna fleet. FOA. Fish. Circular. 982: 1–67.

Juan-Jordá, M. J., J. A. Barth, M. E. Clarke, and W. W. Wakefield. Groundfish species association with distinct oceanographic habitat in the Northern California Current. Fish. Oceanogr. 18: 1–19.

Kimura, S., N. Munenori, and T. Sugimoto. 1997. Migrations of albacore, Thunnus alalunga, in the North Pacific Ocean in relations to large oceanic phenomena. Fish. Oceanogr. 6: 51–57.

Kimura, S., Y. Kato, T. Kitagawa, and N. Yamaoka. 2010. Impacts of environmental variability and global warming scenario on Pacific Bluefin tuna (Thunnus orientalis) spawning ground and recruitment habitat. Prog. Oceanogr. 86: 39–44.

Laurs, R. M., and R. J. Lynn. 1977. Seasonal migration of north Pacific albacore, Thunnus alalunga, into North America coastal waters: distribution, relative abundance and association with Transition Zone waters. Fish. Bull. 75: 795–822.

Laurs, R. M. 1983. The North Pacific albacore—an important visitor to California Current waters. Calif. Coop. Ocean. Fish. 24: 99–106.

Laurs, R. M., and R. J. Lynn. 1991. North Pacific albacore ecology and oceanography. In Wetherall, J. A. (ed.) Biology, oceanography, and fisheries of the North Pacific Transition Zone and subarctic frontal zone. NOAA Technical Report NMFS. 105: 69–87.

Laurs, R. M., R. Nishimoto, and J. A. Wetherall. 1985. Frequency of increment formation on sagittae of North Pacific albacore (Thunnus alalunga). Can. J. Fish. Aquat. Sci. 42: 1552–1555.

Laurs, R. M., and J. A. Wetherall. 1981. Growth rates of North Pacific albacore, Thunnus alalunga, based on tag returns. US. Fish. Bull. 79: 293–302.

Lehodey, P., M. Bertignac, J. Hampton, A. Lewis, and J. Picaut. 1997. El Niño Southern Oscillation and tuna in the western Pacific. Nature. 389: 715–718.

Lehodey, P., F. Chia, and J. Hampton. 2003. Modeling climate-related variability of tuna populations from a coupled ocean-biogeochemical-populations dynamics model. Fish. Oceanogr. 12: 483–494.

Lehodey, P., I. Senina, and R. Murtugudde. 2008. A spatial ecosystem and populations dynamic model (SEAPODYM)-Modeling of tuna and tuna-like populations. Prog. Oceanogr. 78: 304–318.

Leigh, G. M., and W. S. Hearn. 2000. Changes in the growth of juvenile blue-fin tuna (*Thunnus maccoyii*) an analysis of length frequency data from the Australian fishery. Mar. Freshwater. Res. 51: 143–154.

MacFarlane, R. B., and E. C. Norton. 2001. Physiological ecology of juvenile chinook salmon, *Oncorhynchus tshawytscha* at the southern end of their distribution, the San Francisco estuary and the Gulf of the Farallones, California. Fish. Bull. 100: 244–257.

McHugh, J. L. 1952. The food of albacore (*Germo alalunga*) off California and Baja California. Bulletin Scripps Institution of Oceanography. 6:161–172.

Miller, A. J., J. C. McWilliams, N. Schneider, J. S. Allen, J. A. Barth, R. C. Beardsley, F. P. Chavez, T. K. Chereskin, C. A. Edwards, R. L. Haney, K. A. Kelly, J. C. Kindle, L. N. Ly, J. R. Moisan, M. A. Noble, P. P. Niiler, L. Y. Oey, F. B. Schwing, R. K. Sherman, and M. S. Swenson. 1999. Observing and modeling the California Current System. Eos, Transactions, American. Geophysical. Union: 1–10.

Nakamura, H. 1969. Tuna distribution and migration, blank ed. Fishing News, London.

National Oceanographic Data Center (NODC). 2009. World Atlas. Retrieved from http://www.nodc.noaa.gov/cgi-bin/OC5/WOA09F/woa09f.pl.

Neuheimer, A. B., and P. Gronkjaer. 2012. Climate effects on size-at-age growth in warming waters compensates for earlier maturity in an exploited marine fish. Global. Change. Biol. 18: 1812–1822.

Norris, K. 2006. El Niño and the California Current system. AOS. 235: 1–15.

Okamura, A., H. Zhang, N. Mikawa, A. Kotake, Y. Yamada, N. Horie, S. Tanaka, H. P. Oka, and K. Tsukamoto. 2008. Decline in non-native freshwater eels in Japan: Ecology and future perspectives. Environ. Biol. Fish. 81: 374–358.

Otsu, T., and R. N. Uchida. 1959. Sexual maturity and spawning of albacore in the Pacific Ocean. Fish. Bull. 148: 287–305.

Otsu, T., and R. N. Uchida. 1963. Model of the migration of albacore in the North Pacific ocean. Fish. Bull. 63: 33–44.

Panella, G. 1971. Fish otoliths: Daily growth layers and periodical patterns. Science. 173: 1124–1126.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Fish. Bull. 152: 2–83.

Polovina, J. J., D. R. Kobayashi, D. M. Ellis, M. P. Seki, and G. H. Balaz. 2000. Turtles on the edge: Movement of loggerhead turtles (*Caretta carretta*) along oceanic fronts in the central North Pacific, 1997–98. Fish. Oceanogr. 9: 71–82.

Polovina, J. J., E. Howell, D. R. Kobayashi, and M. P. Seki. 2001. The Transitions Zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. Prog. Oceanogr. 49: 469–483.

Pauly, D., and R. S. V. Pullin. 1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fish. 22: 261–271.

Roden, G. I. 1991. Subarctic-subtropical transition zone of the North Pacific large-scale aspects and mesoscale structure. NOAA Technical Report NMFS. 105: 1–39.

Schaefer, K. M., and D. W. Fuller. 2006. Estimates of age and growth of bigeye tuna (*Thunnus obesus*) in the eastern Pacific Ocean, based on otolith increments and tagging data. ITTAC. Bull. 23: 35–46.

Secor, D. H., J. M. Dean, and E. H. Laban. 1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Institute and the Belle W. Baruch Institute for Marine Biology and Coastal Research. 1–85.

Smith, A. C., and J. S. Shima. 2011. Variation in the effects of larval history on juvenile performance of a temperate reef fish. Austral. Ecol. 36: 830–838.

Stocker, M. 2006. Report of the ISC-Albacore Working Group Stock Assessment Workshop. National Research Institute of Far Seas Fisheries. 1–74.

Sugimoto, T., S. Kimura, and K. Tadokoro. 2001. Impact of El Niño events and climate regime shifts on living resources in the western North Pacific. Prog. Oceanogr. 49: 113–127.

Sund, P. N., M. Blackburn, and F. Williams. 1981. Tunas and their environment in the Pacific Ocean: A review. Oceanogr. Mar. Biol. 19: 443–512.

Ueyanagi, S. 1957. Spawning of the albacore in the Western Pacific. Report Nankai Regional Fisheries Research Laboratory. 6: 113–121.

Wells, R. J. D., and J. R. Rooker. 2004. Distribution, age, and growth of young-of-the-year greater amberjack (*Seriola dumerili*) associated with pelagic Sargassum. Fish. Bull. 102: 545–555.

Wetherall, J. A., R. M. Laurs, R. N. Nishimoto, and M. Y. Y. Young. 1987. Growth variation and stock structure in North Pacific albacore. Working paper for the 10th North Pacific Albacore Workshop. Shimizu, Shizuoka, Japan.

Wexler, J. B., S. Chow, T. Wakabayashi, K. Nohara, and D. Margulies. 2007. Temporal variation in growth of yellowfin tuna (*Thunnus albacares*) larvae in the Panama Bight, 1990–97. Fish. Bull. 105: 1–18.

Wexler, J. B., D. Margulies, and V. P. Scholey. 2011. Temperature and dissolved oxygen requirements for survival of yellowfin tuna *Thunnus albacares*, larvae. J. Exp. Mar. Biol. Ecol. 404: 63–72.

Williams, E. H., and S. Ralston. 2002. Distribution and co-occurrence of rockfishes (family–Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. Fish. Bull. 100: 836–855.

Williams, A. J., J. H. Farley, S. D. Hoyle, C. R. Davies, and S. J. Nicol. 2012. Spatial and sex-specific variation in growth of albacore tuna (*Thunnus alalunga*) across the South Pacific Ocean. PLoS ONE 7(6): e39318. doi:10.1371/journal.pone.0039318.

Williams, A. J., B. M. Leroy, S. J. Nicol, J. H. Farley, N. P. Clear, K. Krusic-Golub, and C. R. Davies. 2013. Comparison of daily- and annual-increment counts in otoliths of bigeye (*Thunnus obesus*), yellowfin (*T. albacares*), southern bluefin (*T. maccoyii*), and albacore (*T. alalunga*) tuna. ICES J. Mar. Sci. 70: 1439–1450.

Wilson, C., and D. Adamec. 2001. Correlations between surface chlorophyll sea-surface height in the tropical Pacific during 1997/1998 ENSO event. J. Geophys. Res. 106: 175–188.